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THE TUBIFICIDAE (ANNELIDA, OLIGOCHAETA) OF CAPE COD BAY. II: ECOLOGY AND SYSTEMATICS, WITH THE DESCRIPTION OF *PHALLODRILUS PARVIATRIATUS* NOV. SP.[1]

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The systematics and ecology of marine organisms in Cape Cod Bay are being studied by means of year-round, qualitative and quantitative benthic samples, collected by the Biotic Census which was initiated by the Systematics-Ecology Program (SEP), Marine Biological Laboratory, Woods Hole, Massachusetts. This account is the second of a series which will report on the marine tubificid Oligochaeta of Cape Cod Bay.

Quantitative samples were taken at one mile intervals over the entire bay. The sampling pattern is based on a system of 1 mile square quadrats, identified by four digit numbers (Fig. 2). Samples were taken by a Smith-McIntyre grab (0.10 m^2) at the center (E1) and at each corner (E2 to E5 running clock-wise from E2 in the northeast corner) of every alternate quadrat in the north-south direction. The samples were separated into two fractions by 1.0 mm and 0.5 mm mesh screens and the material narcotized in 0.015% propylene phenoxetol, fixed in 10% formalin (for 48 hours) and stored in 85% ethanol (McKay and Hartzband, 1970). Qualitative samples, treated in the same manner as the quantitative material, were taken from three corners of the quadrats (see Table I and II for exact locations) by epibenthic sled (Ep), clam dredge (C), and naturalist dredge (N). Oligochaeta from 210 sorted 1.0 mm screen fractions have been examined.

The systematics of five of the species of Tubificidae found in Cape Cod Bay (*Peloscolex intermedius* Cook, 1969, *Adelodrilus anisosetosus* Cook, 1969, *Phallodrilus coeloprostatus* Cook, 1969, *Phallodrilus obscurus* Cook, 1969 and *Limnodriloides medioporus* Cook, 1969) and methods of their examination have been dealt with elsewhere (Cook, 1969). In the systematic section of the present account, the ten species found in the bay are listed with the station numbers, including abundance and physical data, at which they occurred. An additional species, *Phallodrilus parviatriatus* nov. sp. is described, *Peloscolex apectinatus* Brinkhurst, 1965 and *Peloscolex nerthoides* Brinkhurst, 1965, are added to the original list,

[1] Contribution No. 234 from the Systematics-Ecology Program.

and the description of *Tubifex longipenis* Brinkhurst, 1965, previously known from a single mature individual, is confirmed and expanded. The ecological section attempts to explain the distribution of the species in relation to the particle size of the substrate.

Systematics and Distribution

Adelodrilus anisosetosus Cook, 1969

Adelodrilus anisosetosus Cook, 1969, pages 13–15, Figure 3.

Distribution: see Table I (A.2).

Remarks: This species is known only from Cape Cod Bay. Breeding individuals were found in January, May, June and November but on the slender data available it is impossible to generalize on the life-history of the species.

Phallodrilus obscurus Cook, 1969

Phallodrilus obscurus Cook, 1969, pages 17–18, Figure 6.

Distribution: Stations 1730-E3 (2 individuals) and 2130-E2 (2 individuals).

Remarks: Known only from Cape Cod Bay. Breeding individuals were found in November only.

Phallodrilus coeloprostatus Cook, 1969

Phallodrilus coeloprostatus Cook, 1969, pages 16–17, Figure 5.

Distribution: see Table I (Ph.1).

Remarks: Known only from Cape Cod Bay. Breeding individuals were found in January, April, May, June, August, September and November, and it would seem that *P. coeloprostatus* is capable of reproduction at any season of the year.

Phallodrilus parviatriatus nov. sp.

Figure 1

Holotype: United States National Museum (USNM) Cat. No. 42015. Cape Cod Bay, Massachusetts, U. S. A. 41° 54.0′ N, 70° 8.6′ W. Depth 17.1 meters. Collected June 11, 1968. (SEP Station number 1412-E4).

Paratypes: USNM 42016. Two individuals, data as for holotype. USNM 42017. Five individuals, 41° 53.5′ N, 70° 10.7′ W. Depth 18.0 m. Collected January 19, 1967. (SEP Sta. No. 1514-E1). National Museum of Natural Sciences, Ottawa, Canada, Cat. No. 3413. One individual, data as for holotype.

Etymology: "parvus" = L. "small"; hence "having a small atrium."

Description: About 9.5 mm long, 0.3 to 0.4 mm diameter anteriorly, 0.48 mm diameter at segment XI, and 0.35 to 0.43 mm posteriorly. Approximately 64 segments. Prostomium rounded, longer than it is wide at peristomium junction.

Clitellum developed on segments X to XII, but only weakly so, or absent, on ventral surface of segment XI. Dorsal and ventral setae similar in number, size and shape: anteriorly each setal bundle contains 3 to 5 bifid setae, 62 to 87 μ long

TABLE I

Distribution of coarse-sand-dwelling Tubificidae: Ph.1 = Phallodrilus coeloprostatus; *A.2* = Adelodrilus anisosetosus; *T.3* = Tubifex longipenis; *P.4* = Peloscolex benedeni; *P.5* = Peloscolex apectinatus; *— = absent; + = present; ? = no data;* ϕ *=* log_2 *particle diameter in mm*

Station number	No. specimens in 1 mm screen fraction (E1–E5) per 0.10 m²					Date	Depth (m)	Median ϕ
	Ph.1	A.2	T.3	P.4	P.5			
0612-E1	2	—	—	30	1	4/24/68	11.0	0.20
0612-E5	—	—	—	1	—	4/24/68	4.3	?
0616-E1	6	—	2	4	—	8/18/69	7.0	0.27
0616-E4	15	—	11	2	—	8/18/69	51.2	?
0616-E5	38	—	24	6	—	8/18/69	8.2	?
0714-E4	—	—	—	32	—	10/16/69	42.4	−0.80
1110-E1	—	—	30	—	—	8/19/69	5.8	0.73
1212-E1	—	—	—	18	—	3/23/69	21.1	0.25
1212-N (at E3)	—	—	—	+	—	3/23/69	16.2	?
1412-E1	40	—	7	82	—	6/11/68	15.6	−0.57
1412-E2	2	—	21	8	—	6/11/68	13.4	?
1412-E3	—	4	232	—	—	6/11/68	11.6	?
1412-E4	67	2	37	796	1	6/11/68	17.1	0.35
1412-E5	—	—	2	80	—	6/11/68	21.1	−0.27
1412-Ep (E4)	—	—	—	+	—	6/11/68	17.1	?
1412-N (E2)	—	—	—	+	—	6/11/68	13.4	?
1510-E1	3	—	—	—	—	9/11/69	3.4	1.37
1514-E1	3	—	9	135	—	1/19/67	18.0	−0.34
1514-E2	—	1	—	35	1	1/19/67	18.3	−0.28
1514-E3	—	—	41	10	—	1/19/67	18.3	?
1514-E4	—	—	2	42	—	1/19/67	18.3	−0.20
1514-N (E4)	—	—	—	+	—	1/19/67	18.3	?
1514-C (E2)	+	—	+	+	—	1/19/67	18.3	?
1530-N (E2)	—	—	—	—	+	11/21/67	11.3	1.83
1612-E1	43	—	158	33	43	5/13/69	8.5	0.48
1714-E4	—	26	25	3	1	1/21/69	18.6	?
1714-C (E3)	—	—	+	+	—	1/21/69	13.7	?
1730-E3	—	—	—	—	9	11/21/67	8.5	0.81
1816-E1	25	8	—	59	20	5/13/69	21.1	0.26
1816-C (E2)	—	—	—	—	+	5/13/69	20.8	?
1910-E1	—	—	2	1	—	5/17/67	6.7	−0.03
1910-E3	—	—	1	—	—	5/17/67	6.7	0.97
1910-N (E3)	—	—	+	—	—	5/17/67	6.7	?
1914-E1	—	—	42	9	—	11/18/68	11.9	0.43
1930-E2	3	10	—	—	—	11/21/67	10.4	0.54
2016-E3	3	—	—	—	—	6/12/68	12.8	?
2016-E4	—	—	—	2	—	6/12/68	18.0	?
2028-E5	—	—	—	—	2	3/21/66	18.3	?
2110-E1	—	—	8	—	—	9/11/69	7.6	0.61
2130-E2	—	—	22	—	—	11/21/67	6.7	1.12
2212-N (E4)	—	—	+	—	—	4/23/68	6.1	?
2318-E4	—	—	—	10	—	10/13/66	15.0	−0.74

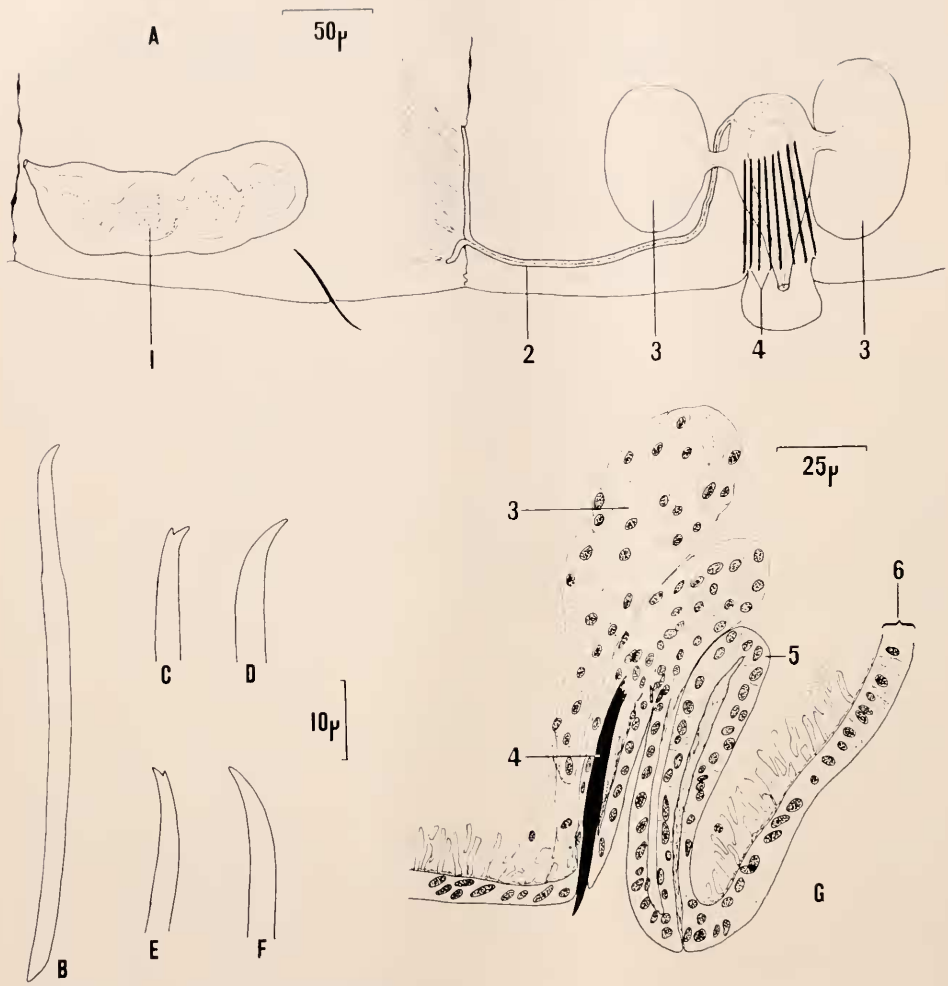

FIGURE 1. *Phallodrilus parviatriatus* nov. sp.; (a.) Lateral view of the genital segments (compiled from dissections); (b.) Penial seta; (c.) Dorsal seta from segment VII; (d.) Dorsal seta from segment XIII; (e.) Ventral seta from segment III; (f.) Ventral seta from segment XII; (g.) Transverse section through the male pore and atrium (USNM 42016): (1.) Spermatheca; (2.) Vas deferens; (3.) Prostate gland; (4.) Penial seta; (5.) Atrium; (6.) Body wall epithelium.

(Fig. 1c and e); posteriorly each bundle contains 2 to 3 simple-pointed setae, 62 to 83 μ long (Fig. 1d and f). Setae bifid with upper teeth shorter than the lower, up to about segment VIII, reaching their maximum length in the region of segments VIII to XV. Ventral setae of segment XI modified into penial bundles each containing 7 to 10 single-pointed setae 75 to 88 μ long (Fig. 1b). Very small, paired, spermathecal pores located at the lateral line of intersegmental furrow IX/X. Paired male pores open on the summits of paired ventro-lateral protuberances just lateral to penial setae.

Coelomocytes small and few in number (but in one paratype from 1514-E4, coelomocytes up to 15 μ diameter were distributed thus: 7 or 8 dorsal in segment VII, 5 dorsal and a clump of 15 to 20 ventrally in segment VIII, 15 to 20 ventral in segment IX, and 7 dorsal in segment X). Pharyngeal glands present up to segment V. Chlorogogen cells begin in segment V. Male genital system (all structures paired—Fig. 1a): relatively large male funnel opens into vas deferens (200 to 220 μ long, 7 to 11 μ diameter in holotype) which runs along the ventral side of segment XI then turns dorsally to join the atrium subapically (antero-dorsally). Atrium erect, elongate pear-shaped, laterally flattened; atrium 84 to 100 μ long and consists of a single layer of cells 5 to 10 μ thick (Fig. 1g); external width of atrium (anterior-posterior direction) 40 to 58 μ, and 26 to 30 μ (lateral direction). Two pear-shaped prostate glands, about 125 μ long, 62 μ wide, join each atrium by thick discrete ducts, one anterior, the other posterior. Paired spermathecae, 133 to 160 μ long 45 to 70 μ wide, situated laterally in the anterior part of segment X: ampullae, which are constricted at intervals giving the appearance of a string of closely-joined spheres, terminate in very small conical ducts; latter open directly to the exterior (*i.e.*, discrete spermathecal ducts absent). Sperm in spermathecae in loose random masses. Median, unpaired, sperm sac extends anteriorly to segment VIII and posteriorly to about segment XIV.

DISTRIBUTION: Stations 1412-E4 (50 individuals); 1514-E1 (3); 1514-E3 (1); 1514-E4 (4).

REMARKS: Known only from Cape Cod Bay. Breeding individuals were found in January and June. *P. parviatriatus* is easily distinguished from other members of the genus by its small erect atria and simple-pointed posterior setae (see Cook, 1969).

Tubifex longipenis Brinkhurst, 1965

Tubifex longipennis Brinkhurst, 1965, page 124, Figure 2j–l. (Typographical error in original.)
Tubifex longipenis. Brinkhurst and Cook, 1966, page 14: Cook, 1969, page 10.

HOLOTYPE: USNM 32605. Five Islands, Dry Point, Georgetown, Maine, U. S. A.

ADDITIONAL MATERIAL: Gray Museum, Marine Biological Laboratory, Woods Hole.

DESCRIPTION: Length 25 to 30 mm, diameter 0.43 to 0.53 mm anteriorly, 0.27 mm posteriorly. Number of segments, 85 to 108. Dorsal and ventral setae similar in number, size and shape: anteriorly each setal bundle contains 2 to 4 broad bifid setae, 110 to 130 μ long, with the upper teeth shorter than the lower; posteriorly, from about segment XII, each bundle contains 1 simple-pointed seta, 110 to 140 μ long, 6.5 to 8.5 μ thick. No modified genital setae.

Pharyngeal glands present in segments IV and V. Atria elongate, tubular, 440 to 510 μ long, 45 to 150 μ diameter, penetrate posteriorly into segment XII. Vasa deferentia, 20 to 23 μ diameter, very long and coiled, join the atria dorsally opposite to the prostate gland opening. Atria terminate in elongate, thickly-cuticularized penes, 320 to 450 μ long, 34 to 73 μ diameter, each of which bears a cuticu-

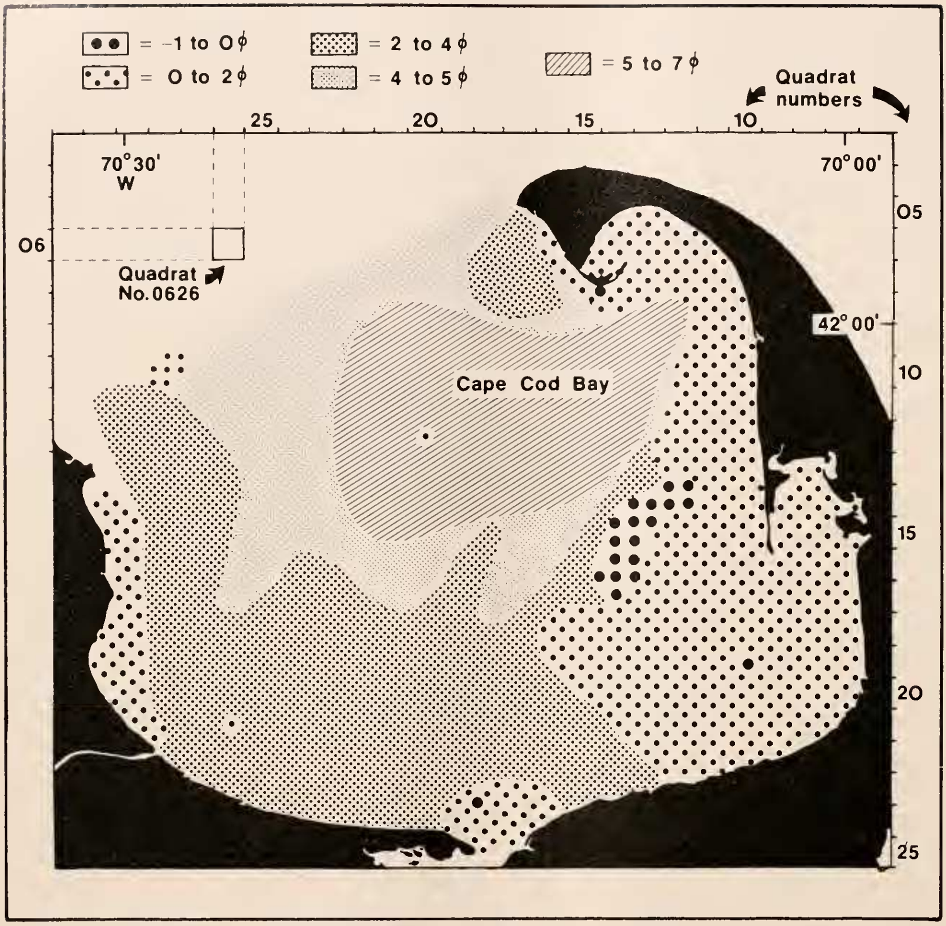

FIGURE 2. Sediment distribution, expressed in terms of median particle size (ϕ units = $\log_2$ particle diameter in mm), in Cape Cod Bay. Sediment analyses were performed mainly on E1 samples, hence the sediment boundries shown may contain errors of about 2 miles in any direction. The marginal figures indicate the system used for quadrat identification.

larized hook about 30 μ long, near its distal end. Paired spermathecae with discrete ducts and sub-spherical ampullae, open just anterior to ventral setae of segment X.

DISTRIBUTION: see Table I (T.3) for Cape Cod Bay; Georgetown, Maine.

REMARKS: The original description (Brinkhurst, 1965) was based on a single specimen. The above description is based on the holotype and additional material from Cape Cod Bay which confirmed the peculiar hooked nature of the penis sheath. Breeding individuals of *T. longipenis* were found in August and September only, and cocoons were present in a January sample which suggests that breeding probably occurs in fall, the cocoons overwinter and hatch the following spring.

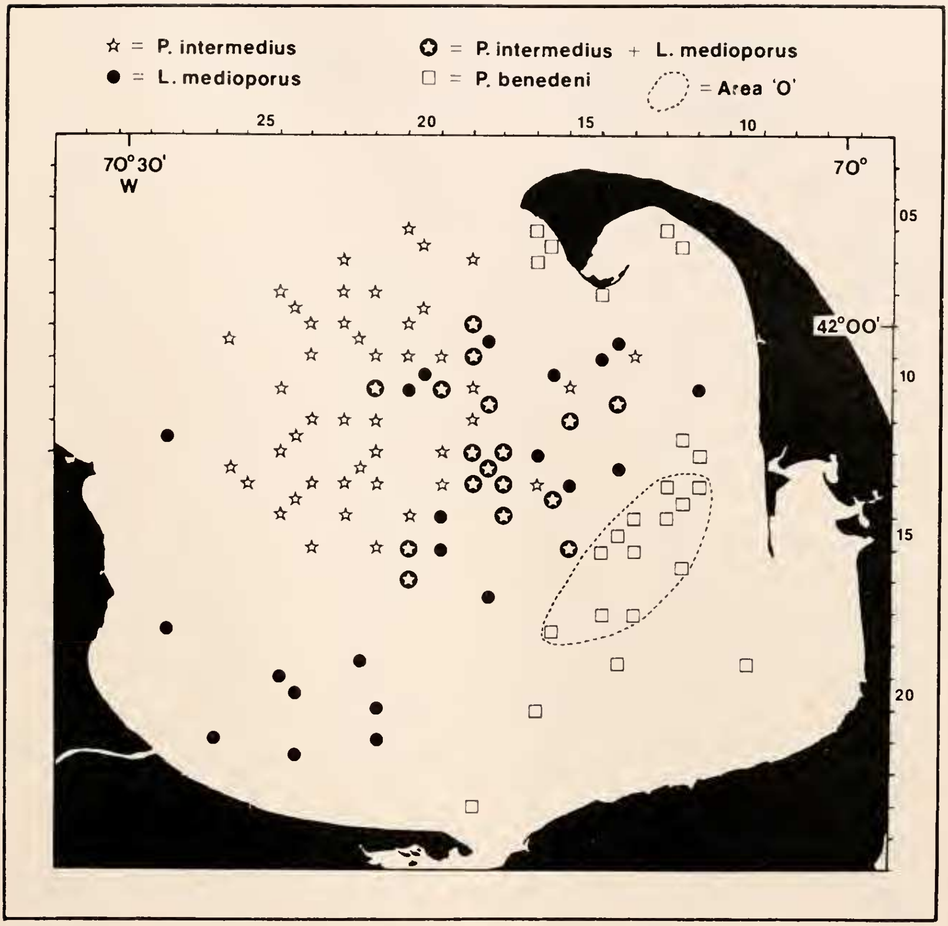

FIGURE 3. Distribution of *Peloscolex intermedius*, *P. benedeni* and *Limnodriloides medioporus* in Cape Cod Bay. The area of maximum species concentration (area "O") is indicated by the dotted line.

Peloscolex benedeni (Udekem, 1855)

Tubifex benedeni Udekem, 1855, page 544.
Peloscolex benedeni (Udekem). Brinkhurst, 1965, page 133; Cook, 1969, page 11. (For full synonomy see Brinkhurst and Jamieson, 1971.)

DISTRIBUTION: see Table I (P.4) and Figure 3 for Cape Cod Bay; Europe; Atlantic coast of North America. A widely distributed species in both brackish-water and fully marine habitats.

Peloscolex apectinatus Brinkhurst, 1965

Peloscolex gabriellae var. *heterochaetus* Brinkhurst, 1965, page 133. (Typographical error in original.)

TABLE II

Distribution of fine-sand and silt-dwelling Tubificidae: P.6 = Peloscolex intermedius; *L.7* = Limnodriloides medioporus; — = *absent;* + = *present;* *?* = *no data;* ϕ = $\log_2$ *particle diameter in mm*

Station number	No. specimens per 0.10 m² (1 mm)		Date	Depth (m)	Median ϕ
	P.6	L.7			
0620-E1	1	—	4/18/67	56.5	4.72
0620-E5	1	—	4/18/67	59.5	?
0620-Ep (E5)	+	—	4/18/67	59.5	?
0718-Ep (E5)	+	—	1/6/69	57.0	?
0722-Ep (E5)	+	—	1/20/69	54.6	?
0722-N (E4)	+	—	1/20/69	53.1	?
0722-C (E3)	+	—	1/20/69	54.3	?
0820-E1	1	—	8/20/68	50.9	5.97
0820-N (E4)	+	—	8/20/68	50.4	?
0824-E1	4	—	6/28/67	49.1	4.63
0824-E3	1	—	6/28/67	49.1	?
0824-E5	1	—	6/28/67	50.0	?
0824-Ep (E3)	+	—	6/28/67	49.1	?
0824-N (E5)	+	—	6/28/67	50.0	?
0914-E1	—	1	2/20/68	31.4	5.95
0914-E4	—	1	2/20/68	33.8	?
0914-N (E3)	+	—	2/20/68	35.1	?
0918-E1	—	70	1/23/68	41.8	5.65
0918-E4	4	5	1/23/68	42.1	?
0918-E5	4	4	1/23/68	45.4	?
0922-E1	8	—	3/27/68	46.4	5.95
0922-E5	2	—	3/27/68	47.6	?
0922-C (E3)	+	—	3/27/68	44.5	?
0926-E1	1	—	6/10/68	47.3	4.17
1012-E3	—	4	9/7/67	21.6	?
1016-E1	—	8	8/19/68	36.0	6.20
1016-N (E3)	+	—	8/19/68	34.2	?
1020-E1	—	1	3/23/67	45.8	6.15
1020-E2	1	—	3/23/67	43.3	?
1020-E3	29	9	3/23/67	42.4	?
1020-E4	—	1	3/23/67	42.7	?
1020-E5	2	—	3/23/67	45.8	?
1020-Ep (E5)	+	—	3/23/67	45.8	?
1020-N (E3)	+	—	3/23/67	42.4	?
1024-E4	16	—	12/19/68	44.5	?
1024-Ep (E2)	+	—	12/29/68	48.5	?
1114-E1	1	19	3/11/69	31.7	5.41
1118-E1	10	8	9/30/68	42.7	6.33
1118-Ep (E4)	+	—	9/30/68	42.4	?
1118-C (E5)	+	—	9/30/68	42.4	?
1122-Ep (E4)	+	—	12/19/68	44.5	?
1122-N (E3)	+	—	12/19/68	43.6	?
1122-C (E2)	+	+	12/19/68	47.3	?
1216-E2	—	4	12/19/67	32.3	?
1216-E4	—	22	12/19/67	32.3	5.82
1216-N (E2)	+	—	12/19/67	32.3	?
1220-E3	3	—	8/26/68	36.9	?
1224-E1	1	—	3/27/68	42.7	4.63

Table II—(*Continued*)

Station number	No. specimens per 0.10 m² (1 mm)		Date	Depth (m)	Median φ
	P.6	L.7			
1224-Ep (E4)	+	–	3/27/68	40.2	?
1224-N (E2)	+	–	3/27/68	43.9	?
1228-E1	–	1	5/10/67	33.2	3.38
1314-E1	–	206	4/23/68	29.9	5.81
1318-E1	1	5	6/14/67	35.7	5.72
1318-E2	2	9	6/14/67	36.6	?
1318-E3	16	42	6/14/67	36.0	?
1318-E4	9	6	6/14/67	35.1	?
1318-E5	43	3	6/14/67	38.4	?
1318-N (E2)	+	–	6/14/67	36.6	?
1322-E1	18	–	7/24/67	36.3	5.31
1322-E2	14	–	7/24/67	40.3	?
1322-E3	3	–	7/24/67	37.5	?
1322-E4	13	–	7/24/67	38.4	?
1322-N (E2)	+	–	7/24/67	40.3	?
1326-E1	1	–	7/22/66	35.7	3.63
1326-Ep (E3)	+	–	7/22/66	36.6	?
1416-E1	1	29	10/1/68	32.0	5.50
1416-Ep (E5)	+	–	10/1/68	32.6	?
1416-C (E2)	–	+	10/1/68	32.0	?
1420-Ep (E2)	+	–	12/12/68	33.9	?
1420-N (E4)	+	–	12/12/68	33.3	?
1420-C (E3)	–	+	12/12/68	32.9	?
1424-E1	1	–	11/19/68	38.1	4.73
1424-E4	1	–	11/19/68	39.4	?
1424-Ep (E2)	+	–	11/19/68	39.4	?
1424-N (E4)	+	–	11/19/68	36.9	?
1518-E2	2	2	1/23/68	34.2	?
1518-N (E2)	+	–	1/23/68	34.2	?
1522-Ep (E5)	+	–	8/19/68	33.2	?
1522-N (E3)	+	–	8/19/68	31.7	?
1616-E2	3	37	4/22/68	28.7	?
1620-E2	–	2	12/19/67	33.2	?
1620-E4	–	1	12/19/67	32.3	?
1620-E5	3	2	12/19/67	32.0	?
1620-Ep (E4)	+	–	12/29/67	32.3	?
1624-E2	1	–	5/13/68	33.5	?
1718-E1	–	4	10/29/68	26.8	4.04
1828-E1	–	8	3/11/69	19.8	4.22
1922-E1	–	1	8/14/67	24.7	3.75
2024-E1	–	1	3/27/68	21.4	3.29
2024-E5	–	1	3/27/68	23.2	?
2122-E2	–	3	1/7/69	26.8	?
2122-C (E3)	–	+	1/7/69	23.8	?
2126-E4	–	9	2/7/66	20.4	2.73
2224-E1	–	6	3/27/69	20.4	2.72

Peloscolex gabriellae var. *apectinata* Brinkhurst, 1965, page 135.
Peloscolex gabriellae apectinata. Brinkhurst and Cook, 1966, page 17.
Peloscolex apectinatus. Brinkhurst and Simmons, 1968, page 187.

DISTRIBUTION: see Table I (P.5) for Cape Cod Bay; Halifax Harbor, Nova Scotia; San Francisco Bay, California.

Peloscolex nerthoides Brinkhurst, 1965

Peloscolex gabriellae var. *nerthoides* Brinkhurst, 1965, page 134.
Peloscolex gabriellae nerthoides. Brinkhurst and Cook, 1966, page 17.
Peloscolex nerthoides. Brinkhurst and Simmons, 1968, page 187.

DISTRIBUTION: Station 0714-E4 (about 400 individuals) in Cape Cod Bay; San Francisco Bay, California.

Peloscolex intermedius Cook, 1969

Peloscolex intermedius Cook, 1969, page 11, Figure 2.

DISTRIBUTION: see Table II (P.6) and Figure 3 for Cape Cod Bay; continental shelf, near the continental slope, south of Martha's Vineyard, Massachusetts (Cook, 1970).

Limnodriloides medioporus Cook, 1969

Limnodriloides medioporus Cook, 1969, page 21, Figure 7.

DISTRIBUTION: see Table II (L.7) and Figure 3 for Cape Cod Bay; continental shelf, south of Martha's Vineyard, Massachusetts (Cook, 1970).

ECOLOGICAL SECTION

Sediment analysis

Mechanical analysis of the sediments in Cape Cod Bay was undertaken by Mr. A. Michael (Systematics-Ecology Program, Marine Biological Laboratory) using graded sieves for the coarse fraction (-1 to $+4\ \phi$) and pipette analysis for the fine fraction; the data, expressed in terms of ϕ units ($\log_2$ particle size in mm) were analyzed by the Woods Hole Oceanographic Institution's Sigma 7 computer. The results reveal that, except for the very coarse sediments (-1 to $+1\ \phi$), there is a general decrease in particle size with increasing depth (Fig. 4).

In the following discussion the median particle size (*i.e.*, median ϕ) is used throughout as a single, convenient parameter expressing the sediment type. Coarse sands (-1 to $2\ \phi$) are restricted to the eastern part of the bay and, in smaller areas, the mouth of Barnstable Harbor and the southwestern edge of the bay. Fine sands (2 to $4\ \phi$) are localized in the southern half, while silts and clays predominate in the central and northern parts of Cape Cod Bay (Fig. 2).

Distribution of the Tubificidae

The occurrence of the ten tubificid species was correlated with depth and the median particle size of the substrate (Table I and II, Fig. 4, and under "Distribution" of various species). These results, together with the mapped distribution of three of the dominant species (Fig. 3), show that the Tubificidae are divisible into two distinct, non-overlapping communities; (1) a fine-sand and silt community (3 to $7\ \phi$) consisting of *Peloscolex intermedius* and *Limnodriloides medio-*

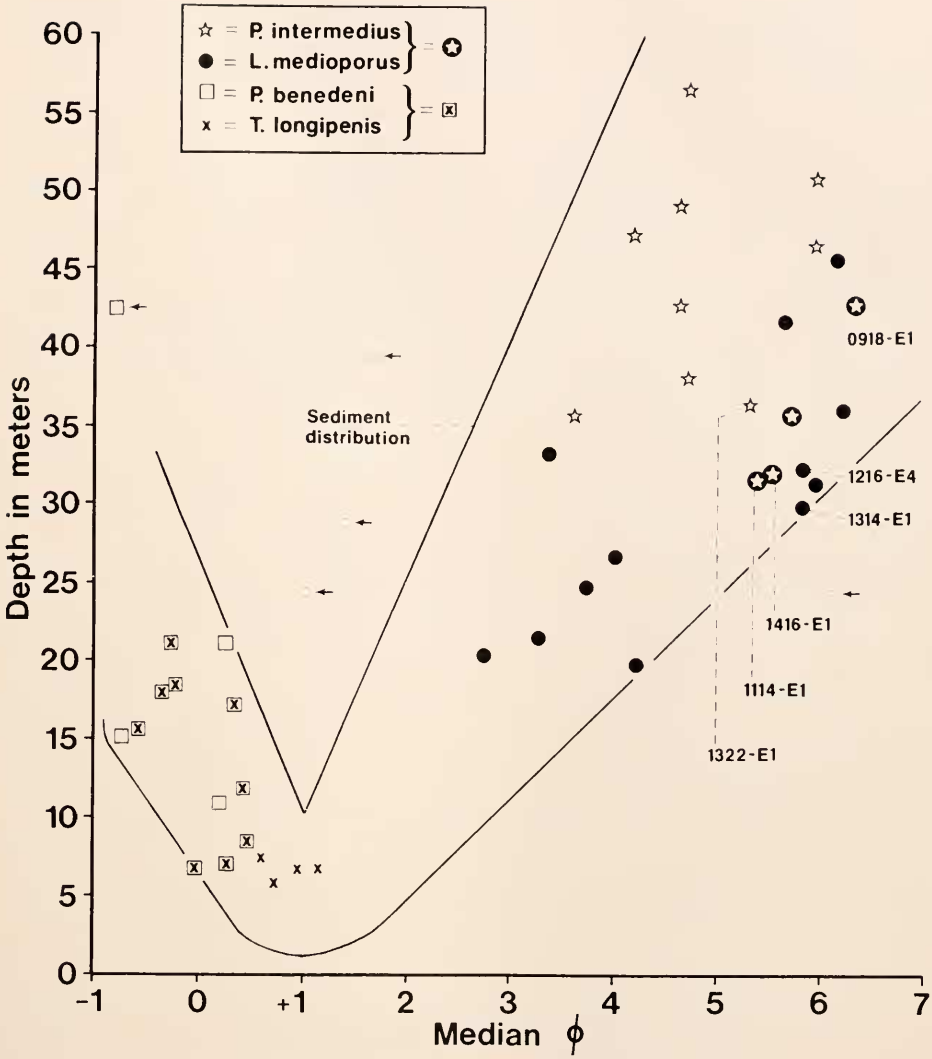

FIGURE 4. Distribution of the four dominant tubificids, *Peloscolex intermedius, P. benedeni, Limnodriloides medioporous* and *Tubifex longipenis*, in relation to the depth and median particle size of the substrate. The outer solid line indicates the outer limits of sediment types in relation to depth, with the exception of five stations (indicated by arrows) which lie outside the limits; a total of 136 stations were analysed for particle size.

porus; (2) a coarse-sand community (−1 to 2 ϕ consisting of *Phallodrilus obscurus, P. coeloprostatus, P. parviatriatus, Adelodrilus anisosetosus, Tubifex longipenis, Peloscolex benedeni, P. apectinatus* and *P. nerthoides.* Depth does not seem to be a limiting factor as the shallow limits of *L. medioporus* overlap with the deeper stations in which *P. benedeni* and *T. longipenis* occur (Fig. 4). The sands with a median ϕ of 1.2 to 2.7 are not inhabited by Tubificidae.

Whilst these two communities are distinctly separate in terms of particle size alone, the distributions of the species within them are more difficult to interpret and, therefore, will be considered separately.

(1) *Fine-sand and silt community*

P. intermedius and *L. medioporus* are the only two tubificids which occur in the finer sediments of Cape Cod Bay. As far as is known both species are unspecialzed infaunal deposit feeders. While apparently utilizing the same resources, the two species coexist in the central part of the bay (Fig. 2). Other such tubificid associations are well-known; *e.g.*, the fresh-water species *Limodrilus hoffmeisteri* and *Tubifex tubifex*. One mechanism for exploiting the same nutritional resource consists of a differential survival of various species of bacteria passing through the gut of different tubificid species (Brinkhurst and Chua, 1969), hence the results discussed below, based on sedimentary parameters, should be regarded as empirical rather than as an explanation of the mechanism of coexistence.

From the available data, the habitat of *P. intermedius* can be defined by depths in excess of 27 m and a substrate with median particle sizes ranging from 3.5 to 6.4 ϕ. *L. medioporus* occurs from 18 to 46 m in depth, and 2.7 to 6.4 median ϕ. The distribution of the two species can be summarized as follows: (1) *P. intermedius* and *L. medioporus* may occur either separately, or, at stations with fine substrates (5.3 to 6.4 ϕ), within the same 0.1 m^2 (Table II; Fig. 3); (2) both species reach their maximum abundance (up to about 2000 per m^2 for *L. medioporus*) in the central part of the bay (Table II) within a narrow range of substrate types, both in terms of median particle size (5.3 to 6.0 ϕ—Table II and Fig. 4), and total substrate composition (sand = 3 to 32%, silt = 50 to 72%, clay = 13 to 30%—Table II and Fig. 5); (3) the zone of maximum abundance physically overlaps the zone of species coexistence but not necessarily within the same 0.1 m^2 (Table II and Fig. 3); (4) both in terms of median particle size (Fig. 4) and total sediment composition (Fig. 5), *P. intermedius* can exist over most of the range of *L. medioporus* though the latter seems to be more tolerant of coarser sediments; (5) *L. medioporus* is often physically separate from *P. intermedius* as it tends to inhabit shallower stations especially when it occurs in the coarser sediments (Fig. 4); (6) *L. medioporus* appears to be absent in intermediate substrates with the median ϕ between 4.3 to 5.3 which are inhabited by *P. intermedius* (Fig. 4); (7) possibly identical to number 6 but stated in different terms, *P. intermedius* can exist in intermediate sediments (defined by median ϕ) with a lower percentage of clay than *L. medioporus* (Fig. 5).

A working hypothesis on the dynamics of this situation can be deduced from these facts, thus: an optimum sediment type, consisting of small particles which probably constitute an abundant food resource, allows *L. medioporus* and *P. intermedius* to coexist in relatively large numbers (1, 2, and 3), *P. intermedius* competitively excludes *L. medioporus* from sediments with average particle sizes only slightly larger than the optimum (6 and 7), and either (a) *L. medioporus* is more successful in exploiting coarser sediments and shallower environments than is *P. intermedius*, thus excluding competitively the latter from such situations, or (b) *P. intermedius* cannot survive depths less than about 25 m (4 and 5). It is impossible, with the present data, to decide whether competitive exclusion, the depth

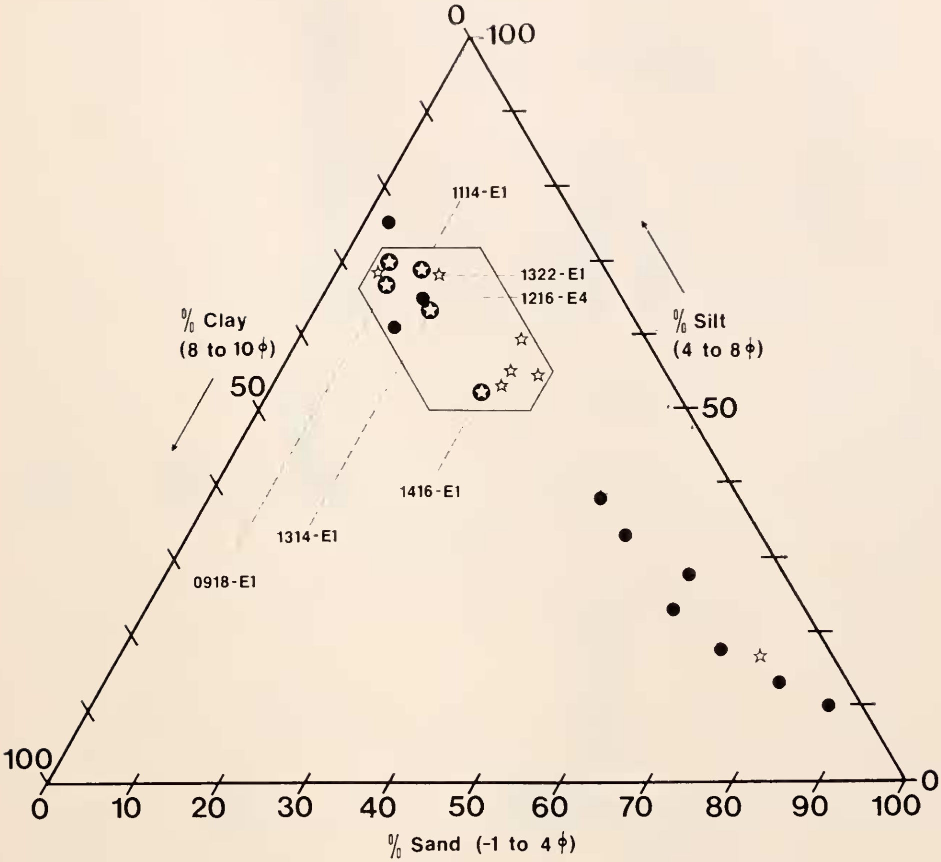

FIGURE 5. Distribution of *Peloscolex intermedius* and *Limnodriloides medioporus* in relation to the total sediment composition measured in percentages of sand, silt and clay. The symbols used for species identification are the same as in Figure 4.

tolerance of *P. intermedius*, or some other factor, is the deciding one in the distribution of this species and *L. medioporus* in the coarser sediments.

(2) *Coarse-sand community*

In the coarse sediments (from −0.80 to 1.83 median ϕ) *P. benedeni* is the dominant tubificid in both frequency and abundance (up to about 8000 per m^2) followed closely by *T. longipenis* (up to about 2300 per m^2) (Table I). The other six species which constitute the coarse-sand Tubificidae (*Adelodrilus anisosetosus, Phallodrilus obscurus, P. coeloprostatus, P. parviatriatus, Peloscolex apectinatus,* and *P. nerthoides*) occur sporadically (Table I and Systematic Section) but often in significant numbers. At any given station only one species may be present, or up to six can occur in association (*e.g.*, 1412-E4 where the total abundance of Tubificidae is about 10,000 per m^2; this is probably a low estimate because many,

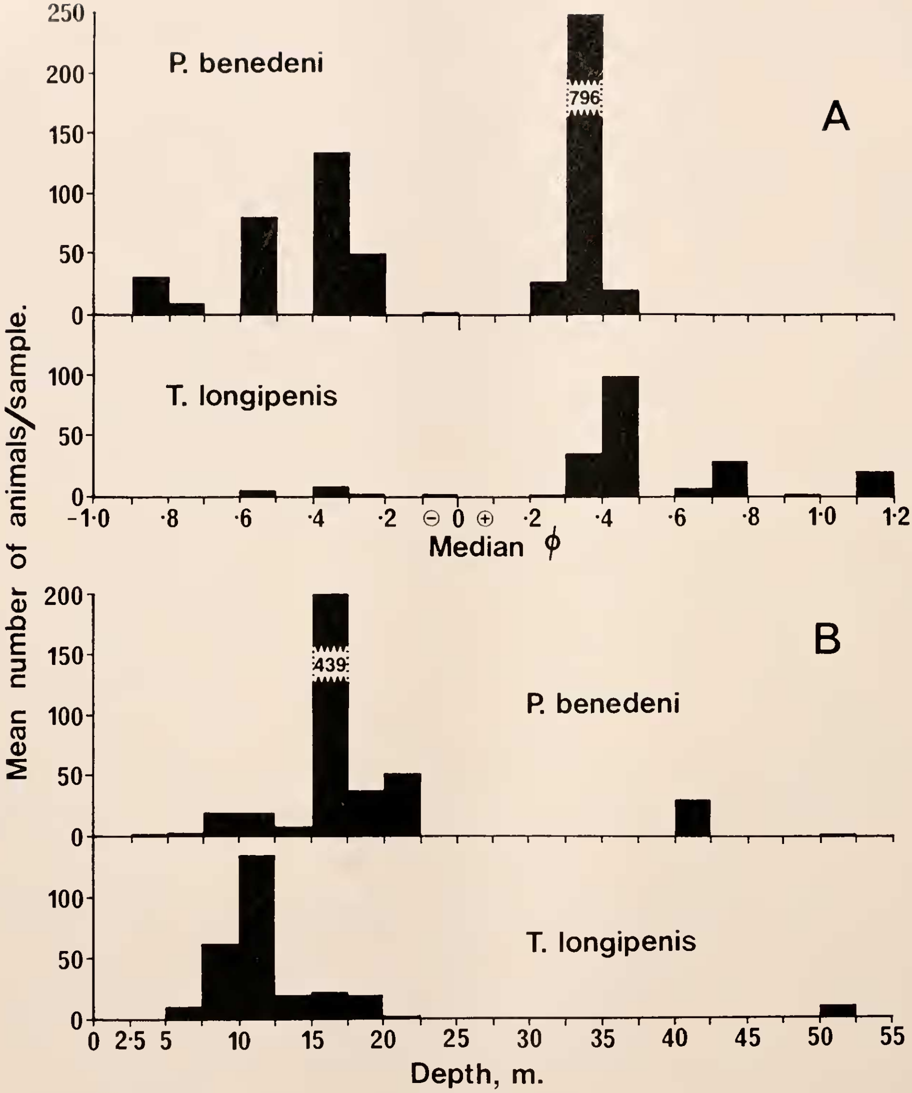

FIGURE 6. Histograms of the mean number of *Peloscolex benedeni* and *Tubifex longipenis* occurring in each quantitative sample in relation to two parameters: (a.) Median particle size (system of 0.1 ϕ classes used); (b.) Depth (2.5 m classes).

if not the majority, of the smaller species may not have been retained by the 1.0 mm screen).

In this section the two dominant species will be considered together, and brief notes on the other six, for which data are rather sparse, discussed separately. This arrangement is also convenient and fortunate from the biological viewpoint because *P. benedeni* and *T. longipenis* are probably both free-burrowing forms, being the counterparts of *P. intermedius* and *L. medioporus* in the fine-sands and silts, while all, or some, of the other six species, because of their small size, are likely to be members of the true interstitial fauna.

P. benedeni and *T. longipenis*

The distribution patterns of *P. benedeni* and *T. longipenis,* and their interpretation, bear some resemblance to those of *P. intermedius* and *L. medioporus.* The habitat of *P. benedeni* in Cape Cod Bay is characterized by depths between 4.3 to 51.2 m, and a substrate with the median particle sizes between −0.80 to 0.48 ϕ; *T. longipenis* is found in depths between 5.8 to 51.2 and in sediments of −0.57 to 1.12 median ϕ. The distribution of the two species can be summarized as follows: (1) *P. benedeni* and *T. longipenis* occur either separately, or within the same 0.1 m^2 (Table I); (2) in terms of the median particle size of the sediment, *P. benedeni* is most abundant around 0.3 to 0.4 ϕ, and *T. longipenis* between 0.4 to 0.5 ϕ (Fig. 6a); (3) *P. benedeni* occurs in high numbers in sediments coarser than 0.3 ϕ (especially between −0.6 to −0.2 ϕ) while *T. longipenis* has secondary peaks of abundance in sediments finer than 0.5 ϕ (between 0.6 to 1.2 ϕ) (Fig. 6a); (4) in terms of depth, *P. benedeni* reaches its maximum abundance between 15 to 22.5 m, while 81% of the *T. longipenis* population exists between 2.5 to 15 m (Fig. 6b); (5) *T. longipenis* tends to occur alone in the finer substrates at the shallower stations (Fig. 4); (6) in terms of total sediment composition, all stations at which either, or both, species occur, lie in the category of sand = 97 to 100%, silt = 0 to 2% and clay = 0 to 1.8%.

These differences between the distributions of *P. benedeni* and *T. longipenis* may be interpreted as follows: the two species may coexist over a wide range of coarse sediments but *T. longipenis* seems more able to exploit those with finer particles which tend to occur at shallower stations (Fig. 4), possibly excluding *P. benedeni* from them. Similarly they can exist together over a wide depth range; the deep limits in Cape Cod Bay are probably set by the distribution of suitable sediments (Fig. 4); the shallow depth limits *per se,* contrary to the implication of Figure 6b, are not thought to be controlling factors because of the high correlation between depth and sediment composition (Fig. 4), and the fact that *P. benedeni* is known to extend well up into the littoral zone in other localities (Moore, 1905; Lasserre, 1967).

Remaining coarse-sand Tubificidae

Little can be said concerning the remaining six species on the limited data available; all occurred within the depth and median particle size ranges of the two dominant species, except *Phallodrilus coeloprostatus* (see below and Table I). Geographically the majority of these species were concentrated in a small ovoid area of Cape Cod Bay whose major axis runs from 1412-E2 in the northeast, to 1816-E1 in the southwest (Fig. 3). The upper two-thirds of this area corresponds to the concentration of very coarse sediments (−1 to 0 ϕ; Fig. 2).

Phallodrilus coeloprostatus: This species, next in order of numerical importance after *P. benedeni* and *T. longipenis,* occurred at fourteen stations, at eleven of which it was associated with *P. benedeni.* It extends into slightly finer sediments (1.37 ϕ) than the two dominant species and, like these, its lower depth limit in the bay (51.2 m) is probably a function of substrate availability. Geographically *P. coeloprostatus* occurred within or near the ovoid area of maximum species concentration (hereafter called area "0"), a small near-shore area at the northwestern tip of Cape Cod (0616), and an isolated area near the western shore (1930).

Phallodrilus parviatriatus: P. parviatriatus occurred at only four stations where both *P. benedeni* and *T. longipenis* were also found and which all lie within area "0."

Phallodrilus obscurus: This species was found at only two stations located close to the western shore (6.7 and 8.5 m depth). It may be significant that both stations have relatively fine sediments (0.81 and 1.12 median ϕ) and that the *P. benedeni* population appears to be absent from this part of the bay.

Adelodrilus anisosetosus: Five out of the total of six stations at which this species occurred lie within area "0"; the isolated station on the western shore, like the other five, lie within the range, median $\phi = -0.28$ to 0.54, depth = 10.4 to 21.1 m.

Peloscolex apectinatus: The species was represented at six stations in area "0," at one station near the bay's northeastern edge, and at three stations along the western shore. All of these stations are shallower than 22 m and have median particle sizes finer than $-0.3\ \phi$.

Pelescolex nerthoides: This was found at only one station (0714-E4), but in considerable numbers (4000 + per m^2), at a depth of 42.4 m and in a very coarse sediment (-0.8 median ϕ).

Discussion

As a basis for discussion the major conclusions of the ecological section may be summarized as follows: within Cape Cod Bay two different communities of Tubificidae occur; species distribution, between and possibly within communities, is related to the median particle size of the sediments; (1) *P. intermedius* and *L. medioporus* constitute a free-burrowing, fine-sand and silt community; (2) *P. benedeni* and *T. longipenis* play the dominant role in a coarse-sand community which may be subdivided into (a) a free-burrowing component composed of the two dominant species, and (b) an interstitial component composed of six species characterized by their small size.

Marine Oligochaeta are not well-known and factors influencing their distribution have been little studied. Lasserre (1967) in an analysis of some littoral Enchytraeidae and Tubificidae concluded that their distribution was correlated with the median particle size of the substrate and the percentage of sediment under 80 μ (3.64 ϕ) in diameter. Lasserre (1967) found *P. benedeni* in sediments with median particle sizes ranging from -1.0 to 1.74 ϕ (compared to -0.8 to 0.48 ϕ in the present study), at densities up to 1,000,000 per m^2 in the finer sediments with 7 to 10% of the particles smaller than 3.64 ϕ: densities declined in coarser substrates and as the percentage of particles smaller than 3.64 ϕ declined. In the present study, high densities of *P. benedeni* also tended to occur in the finer sediments: the fact that *P. benedeni* was not found in sediments finer than 0.48 ϕ (compared to 1.74 ϕ in Lasserre's work), supports the hypothesis that the species may be competitively excluded by *T. longipenis* in the finer sediments.

Other authors mentioning sediment types in relation to marine or littoral Oligochaeta include Bülow (1957) who demonstrated that zones of differing substrata supported different oligochaete faunas, Brinkhurst and Kennedy (1962) who found that the relative abundance of three tubificids was controlled in part by the substrate, and Brinkhurst (1964a) who noted that *Tubifex costatus* (Claparède, 1863) inhabited a wide variety of sediment types.

The fresh-water Tubificidae, however, have been better studied, especially in recent years: species distribution and/or abundance is controlled, according to Ravera (1951) by the organic content of the sediment, Henson (1963) stated that factors other than inorganic parameters are operative, and Brinkhurst (1962; 1964b) concluded that, while the depth and the nature of the substrate may be determinants of some species distributions, biotic factors (interspecific competition and predation) are probably the most important. Valle (1927), Rzoska (1936), Szczepanski (1953), Della Croce (1955), Korn (1963) and Wachs (1967; 1968) have all shown a positive correlation between species distributions and inorganic sediment characteristics in fresh-water.

Thus, many of the studies on both fresh-water and marine Tubificidae have concluded that a correlation exists between the substrate type and the distribution and/or abundance of species. This work reports similar results, but Brinkhurst (1962) has pointed out that observed species distributions, however closely they may seem to be correlated with sediment types, may be a reflection of some other factor such as the distribution of predators. This is especially true in the case of the marine Oligochaeta, a group about which such basic information as, their tolerance to physical conditions, their specialized food requirements, and the identity of their predators, is still unavailable. However, despite these reservations, the results discussed here, whilst failing to elucidate definitively the autecology of the Tubificidae in Cape Cod Bay, do have an empirical validity which, for a rather obscure but ecologically significant group of marine animals, may be sufficient justification for their presentation.

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Summary

(1) Ten species of Tubificidae are recorded from Cape Cod Bay, as follows: *Adelodrilus anisosetosus, Limnodriloides medioporous, Peloscolex apectinatus, P. benedeni, P. intermedius, P. nerthoides, Phallodrilus coeloprostatus, P. obscurus, P. parviatriatus* and *Tubifex longipenis*.

(2) *Phallodrilus parviatriatus* nov. sp. is characterized by small erect atria and simple-pointed posterior setae.

(3) The original description of *Tubifex longipenis* Brinkhurst, 1965, is confirmed and expanded.

(4) On the basis of species distributions in relation to sediment types, two major tubificid communities are recognized.

(5) *P. intermedius* and *L. medioporus* constitute a free-burrowing, fine-sand and silt community (median particle size of the substrate between 3 to 7 ϕ).

(6) *P. benedeni* and *T. longipenis* are the free-burrowing components of a coarse-sand community (-1 to 2 median ϕ) which also contains *A. anisosetosus, Peloscolex apectinatus, P. nerthoides, Phallodrilus coeloprostatus, P. obscurus* and *P. parviatriatus;* some, or all, of the last six species are probably interstitial.

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